2018

Biotic consequences of a shift in invertebrate ecosystem engineers: Invasion of New Zealand rocky shores by a zone-forming ascidian

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Publication Details

Davis, A. R., Walls, K. & Jeffs, A. (2018). Biotic consequences of a shift in invertebrate ecosystem engineers: Invasion of New Zealand rocky shores by a zone-forming ascidian. Marine Ecology, 39 (3), e12502-1-e12502-10.

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The pervasive effects of invasive ecosystem engineers, that is those species that modify their environment, are well documented, but rarely have the broader impacts of one foundation invertebrate species being replaced by another been examined. In New Zealand, green-lipped mussels, Perna canaliculus, commonly dominate wave-exposed rocky shores. The recent appearance of an invasive ecosystem engineer, the ascidian Pyura doppelgangera, at the very northern tip of New Zealand now threatens to exclude these bivalves from this habitat. Here, we report major shifts in assemblages associated with the invader and chronicle its continued spread. We examined epibiota associated with clumps of mussels and clumps of Pyura from two rocky shore habitats-pools and emergent substrata at two locations. We detected some differences in species richness in biota associated with the two foundation species, but faunal abundance only differed between the locations. These minor changes were dwarfed by the shift in species composition within clumps of each foundation species. Molluscs, particularly gastropods, and crustaceans dominated the assemblage within mussels. In contrast, tubicolous polychaetes dominated the fauna associated with the ascidian. Sessile epifauna, notably barnacles and calcareous tube-dwelling polychaetes, were common on mussels, but never encountered on the ascidian. Multivariate analysis revealed marked dissimilarity (>80%) between the characteristic mussel and ascidian faunas with virtually no overlap. This biotic shift overshadowed any differences between habitats and locations. The broader implications of these faunal shifts for local and regional patterns of biodiversity, as well as ecosystem function, remain unclear, but deserve further attention.

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Biotic consequences of a shift in invertebrate ecosystem engineers: invasion of New Zealand rocky shores by a zone-forming ascidian

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Abstract

The pervasive effects of invasive ecosystem engineers, that is those species that modify their environment, are well documented, but rarely has the broader impacts of one foundation invertebrate species being replaced by another been examined. In New Zealand, green-lipped mussels, *Perna canaliculus*, commonly dominate wave-exposed rocky shores. The recent appearance of an invasive ecosystem engineer, the ascidian *Pyura doppelgangera*, at the very northern tip of New Zealand now threatens to exclude these bivalves from this habitat. Here we report major shifts in assemblages associated with the invader and chronicle its continued spread. We examined epibiota associated with clumps of mussels and clumps of *Pyura* from two rocky shore habitats - pools and emergent substrata at two locations. We detected some differences in species richness in biota associated with the two foundation species, but faunal abundance only differed between the locations. These minor changes were dwarfed by the shift in species composition within clumps of each foundation species. Molluscs, particularly gastropods, and crustaceans dominated the assemblage within mussels. In contrast, tubicilous polychaetes dominated the fauna associated with the ascidian. Sessile epifauna, notably barnacles and calcareous tube-dwelling polychaetes were common on mussels, but never encountered on the ascidian. Multivariate analysis revealed marked dissimilarity (>80%) between the characteristic mussel and ascidian faunas with virtually no overlap. This biotic shift overshadowed any differences between habitats or locations. The broader implications of these faunal shifts for local and regional patterns of biodiversity, as well as ecosystem function remain unclear, but deserve further attention.

INTRODUCTION

Foundation species often play a fundamental role in shaping habitat for a range of associated taxa, thereby creating the structural and functional diversity of ecosystems and perhaps ensuring their resilience (Coleman and Williams 2002). These ecosystem engineers exert their influence by either directly modifying the physical environment or altering biotic interactions. For example, on rocky shores populations of attached mussels alter the physical environment by providing more complex habitat structure as a result of the spatial arrangement of their hard shells (Commito et al. 2008). This structure may directly affect organisms within the interstices of the mussel matrix by ameliorating environmental extremes, providing refuge from predators and modifying nutrient dynamics (Reush et al. 1994; Crooks 1998).

As ecosystem engineers modify the system of which they are a part, changes in their abundance or their loss from a system often have pervasive effects (Jones et al. 1994). These changes may in turn ripple through the trophic levels in an ecosystem (Crooks 2002). Introduced taxa may assume this engineering role, providing habitat structure where previously it was lacking (e.g., Heiman et al. 2008). For example, the appearance of an invasive ascidian on the rocky shores of northern Chile has extended the distribution of invertebrates into the mid-intertidal zone thereby increasing rocky shore diversity (Castilla et al. 2004).

While the addition of structure-forming species and the positive effects on biodiversity and abundance has received considerable attention (Jones et al. 2010), the repercussions of replacing one foundation species with another have seldom been explored, at least among animals. These affects on biodiversity are important as an understanding of ecological pattern is the precursor to exploring the underlying processes (Underwood et al. 2000) and has implications for the successful management of invaders. The appearance of an ascidian invader in northern New Zealand presented an opportunity to explore the biotic consequences of changing foundation species in the lower

intertidal zone of temperate rocky shores. A large clump-forming intertidal ascidian was first observed in the remote northern tip of New Zealand in 2007 (Hayward and Morley 2009). It was initially identified as *Pyura praeputialis*, the common intertidal ascidian of south-eastern Australia. Molecular approaches and morphological examination have now confirmed that it is a member of a southern hemisphere species complex comprising at least 5 species. Now identified as *Pyura doppelgangera* Rius and Teske (2013), in recognition of its propensity to closely resemble another - a doppelganger - its native habitat is the southern shores of Bass Strait (i.e., the northern Tasmanian coast) in southern Australia.

Hayward and Morley (2009) suggested that *P. dopplegangera* had been present in northern New Zealand for at least 10 years. They correctly recognised that *P. dopplegangera* was an aggressive occupier of space and saw the potential for this species to become a major zone-forming species on the rocky intertidal shores of New Zealand. It has now been recorded at more than 22 locations in northern New Zealand (Jones et al. 2012; and author's pers. obs.) and continues to invade suitable habitat to the south of its current range; on occasions forming thick bands on the lower shore (authors' pers. obs.). The appearance of this invader is also of concern to the local indigenous (Maori) people as it has the potential to threaten the abundance of *kaimoana* (seafood) and the cultural, recreational and commercial values of New Zealand seashores.

The nature of ecological interactions is often context-dependent with contrasting ecological pattern and processes operating in differing habitats (Lubchenco 1978; Gribben et al. 2013). Indeed, much of our understanding of marine ecological processes is dominated by early studies undertaken on emergent substrata – areas of rocky shore exposed at low tide. Here, we sought to explore how changes in foundation species affected the associated organisms in two distinct intertidal habitats; emergent substrata and shallow intertidal pools. While pools exhibit lower amplitude abiotic fluctuations, they often exhibit large spatial variation in community structure owing to the features associated with individual pools (reviewed by Metaxas and

Scheibling 1993). Rock pools also often support greater species richness (Firth et al. 2013) and more intense biotic relationships would be expected.

Here we assess the community-wide outcome of a shift from one ecosystem engineer (the habitat-forming mussel *Perna canaliculus,* Gmelin) to another filter-feeding ecosystem engineer (the habitat-forming ascidian *Pyura doppelgangera,* Rius and Teske). Clearly it would be unethical to introduce this invader to new locations; hence we have relied on a correlative approach. Given differences in the substratum they present (a hard calcareous shell for the mussel and a 'rubbery' proteinaceous tunic for the ascidian) we anticipated shifts in associated fauna. We predicted that species reliant on hard surfaces such as calcareous tubeworms, barnacles and perhaps algal species would be strongly negatively affected by the appearance of the invader, while taxa using the interstices between clump-forming individuals would not change.

METHODS

Study locations and experimental design

Our focus was on biodiversity associated with the two habitat forming species – the ascidian *Pyura doppelgangera* (*Pyura* hereafter) and the green-lipped mussel *Perna canaliculus* (*Perna* hereafter). We sampled at two reef locations in Northland, on New Zealand's wave exposed western coastline. Shipwreck Bay (35° 10' 37"S, 173° 7' 57"E) at the southern end of Ninety Mile Beach, and Tauroa Peninsula (35° 10' 8"S, 173° 6' 32"E) several km further to the west (Fig. 1). *Pyura doppelgangera* was well established at these locations having been first observed there in 2009 (MPI, pers. comm.). However, *Pyura* did not form extensive sheets at these locations, as seen at some sites further to the north (Fig. 2a) but formed patches that were generally intermingled with clumps of mussels (Fig. 2b).

We sampled within two habitats at the same tidal height, ≈0.2m; shallow pools and emergent substrata (i.e., rock exposed at low tide). In each habitat at each location we removed a 10 x10 cm patch of the mussel and the ascidian (n=5) with a paint scraper as this was the scale over which patches of these

159 foundation species occurred (Fig. 2b); an appropriate 'ecological' quadrat size
160 (Krebs, 1989). A total of 40 samples were collected, frozen within 2 hrs of
161 collection and returned to the lab for later analyses.
162
163 In the laboratory, samples were defrosted and clumps of mussels or ascidians
164 were pulled apart and washed over a 0.5 mm sieve. Individuals from clumps
165 were measured and then carefully examined to ensure that all epibiota had
166 been dislodged. The dislodged fauna was enumerated and identified to the
167 lowest taxonomic level possible. The presence of epiflora (e.g., coralline
168 algae) and sessile fauna (e.g., barnacles and calcareous tubeworms) on the
169 valves of the mussels and test of *Pyura* was also noted and converted to the
170 proportion of individuals in each the clump bearing these epibiota.
171
172 ***Statistical analyses***
173 We used univariate approaches to assess differences in total species
174 richness and the abundance of motile taxa as well as the responses of some
175 individual taxa to the factors of interest. We used a three factor ANOVA;
176 Location (random with two levels; Shipwreck Bay and Tauroa Peninsula),
177 Habitat (fixed with two levels; pools and emergent substrata) Taxon (fixed with
178 two levels; *Pyura* and *Perna*). Prior to analyses, data were assessed visually
179 for normality and a Cochran's C test used to confirm that variances were
180 homogenous. Where differences were detected we used SNK tests for post-
181 hoc pair-wise comparisons (GMAV5, University of Sydney). Data were
182 transformed when required and where appropriate data were pooled in the
183 ANOVA following the pooling procedures outlined by Underwood (1997).
184 Percentage data were arcsin transformed.
185
186 The entire data set was also examined using PERMANOVA, based on Bray
187 Curtis dissimilarity measures (Primer V7). The factors considered were the
188 same as in the univariate analysis above. Data were visualised with an nMDS
189 ordination plot. We also examined the contributions of various taxa to
190 dissimilarity between factors with a SIMPER analysis and report outcomes for
191 taxa that contributed more than 5% to the overall dissimilarity.
192

RESULTS

A total of 54 taxa were recorded from within clumps of *Pyura* and the mussel *Perna*; this included 7 alga species, 21 mollusc species and 5 decapod species. These estimates of species richness were biased low as we were forced to group some taxa which were difficult to distinguish given their size (e.g., chitons in the family Acanthochitonidae and some species of errant polychaetes). Differences in the species richness of the fauna and flora associated with clumps of the invasive *Pyura* and the native *Perna* were variable, but not marked (Fig. 3); these differences were complex as revealed by a three-way interaction in the ANOVA ($F_{1,32}$=4.91 P=0.034, Table 1). Posthoc testing confirmed that the only significant difference in species richness between *Pyura* and *Perna* was in pools at Shipwreck Bay where diversity was more than 50% higher among mussels. No other significant difference in the diversity of associated fauna was apparent for the two foundation species.

The abundance of associated fauna ranged from an average of almost 33 individuals per clump to more than 65 individuals per clump (Fig. 3). Location was the only factor that was significant in the analysis, despite the considerable range in abundance observed. ANOVA confirmed that the abundance of associated fauna was significantly higher at Shipwreck Bay than Tauroa ($F_{1,32}$=5.21 P=0.03, Table 1). We observed that abundance was lower in pools when compared to emergent substrata, but these effects were not significant. Furthermore, no significant interactions were apparent.

Stark shifts in community structure were apparent between fauna associated with *Perna* and those with the *Pyura*. Molluscs and decapod crustaceans dominated the assemblage associated with the native mussel, *Perna*. These abundance of these taxa constituted between 55% and 85% of the fauna within clumps of *Perna* on average, but just 20% to 50% of the fauna associated with *Pyura* (Fig. 4A); a highly statistically significant effect ($F_{1,33}$=57.9 P<0.0001, Table 2).

Polychaetes dominated the fauna associated with *Pyura;* they constituted 35% to more than 50% of the total abundance. In contrast, they did not comprise more than 10% of the abundance of the fauna sampled from *Perna* (Fig, 4B). These differences in abundance were also highly statistically significant ($F_{1,33}$=120.1 P<0.0001, Table 2). Sipunculids were another taxon commonly associated with *Pyura*, but they were never observed in the clumps of Perna (Fig 5). The sipunculid data violated the normality assumption of ANOVA and were not analysed.

As we anticipated, sessile fouling species were restricted to the valves of *Perna* and were not seen on *Pyura*. These included the barnacles, *Chaemosipho brunnea* and *C. columna*, and polychaetes forming calcareous tubes; *Galeolaria hystrix*, *Salmacina* sp. and spirorbids (Fig. 6). The coralline alga, *Corallina officinalis*, showed a particularly complex pattern of distribution. It was largely restricted to the valves of *Perna* in shallow pools while a high proportion of clumps of *Pyura* possessed coralline algae irrespective of habitat (Fig. 6).

The multivariate analysis further underscored the community-wide shifts highlighted by the univariate analyses. nMDS showed very clear separation between fauna associated with the two foundation taxa, while there was considerable overlap between the two habitats for each taxon (Fig. 7). The PERMANOVA revealed a significant 3-way interaction among the factors (Pseudo-$F_{1, 32}$ = 2.914 P=0.005, Table 4). Our interpretation did not change irrespective of whether the PERMANOVA was on untransformed or transformed (presence-absence) data. Some tests had low numbers of unique permutations and should be regarded with caution (Table 4). The *Perna*-associated and *Pyura*-associated assemblages showed a high level of dissimilarity (82.4%). Of the six species contributing more than 5% to this overall dissimilarity three were molluscs and two were polychaetes, although one of the later was lumped from several taxa (Table 5).

DISCUSSION

Our findings clearly demonstrate ecosystem-wide shifts associated with the invasive ascidian, *Pyura doppelgangera*, in northern New Zealand. We predicted that fouling organisms associated with the valves of *Perna*, such as barnacles, would disappear from the assemblage associated with *Pyura*, but we did not expect such a large shift in the motile fauna. Crabs and molluscs dominated clumps of the mussel *Perna canaliculus*, while tubiculous errant polychaetes, occupying sediment tubes, dominated clumps of the ascidian. The shift was statistically significant with the abundance of errant polychaetes accounting for <10% of the sample from *Perna* and exceeding 50% of that from *Pyura*. Other than differences between locations, there were no changes in the overall abundance of invertebrates. Simberloff (2011) has argued that such composition changes constitute "ecosystem impacts" as they will inevitably result in changes to processes such as nutrient cycling.

As we predicted, slow-moving or sessile taxa normally associated with hard surfaces (mussel shell), including limpets in the genus *Notoacmea*, barnacles and calcareous tube-dwelling polychaetes (e.g., spirobids), were absent on the tunic of the invasive *Pyura*. In contrast, these taxa were usually present on a high proportion of the valves of *Perna* within a clump. Surprisingly, Castilla et al. (2004) report the presence of spirorbids and a balanoid barnacle on the invasive *Pyura praeputialis* in Chile. We had also predicted that algal species would be absent or present in low abundance on *Pyura* given the assumed difficulty in attaching to the softer test of this ascidian. We found no evidence in support of this notion, at least for coralline algae; *Corallina officinalis* was more commonly associated with the *Pyura* than *Perna*, irrespective of the habitat examined. The presence of *C. officinalis* on *Pyura* suggested that attachment was not an issue, but protection from desiccation may drive the abundance of the alga on this ascidian.

Ecosystem-wide shifts in diversity and abundance following the addition of structurally complex habitat have been well documented (e.g., Crooks 1998). Ascidians in the genus *Pyura* can form thick bands on temperate rocky shores of the southern hemisphere (Ruis et al. 2017). Fauna occupying the

294 interstices of beds of the closely related intertidal pyurid ascidian *Pyura*
295 *praeputialis* (formerly *P. stolonifera*) have been examined in southern Africa
296 (Fielding et al. 1994), southeastern Australia (Monteiro et al. 2002) and
297 northern Chile – where they have invaded approximately 70 km of coastline at
298 Antofagasta (Cerda and Castilla 2001, Castilla et al. 2004). These studies
299 confirm the high diversity of fauna associated with these zone-forming
300 animals with between 45 and 96 macro-invertebrate taxa. Importantly, where
301 fauna was examined in the laboratory, polychaetes were the dominant taxon
302 in intertidal beds of these pyurid ascidians. In South Africa polychaetes
303 accounted for 30% of the invertebrate abundance (Fielding et al. 1994)
304 compared to between 40% to almost 60%in our study. While in Chile, virtually
305 all of the polychaete species recorded were restricted to the ascidian clumps.
306 Further comparison with our findings are difficult to draw from the work in
307 Chile as these studies contrasted fauna in the ascidian clumps with that on
308 bare substrata (rock), although in Chile *P. praeputialis* has displaced native
309 mussels (Caro et al. 2011).
310
311 Another interesting pattern to emerge from the work in Chile and South Africa
312 in relation to our findings was the high biomass of intertidal sponges observed
313 in these studies. We rarely encountered sponges, but they constituted
314 between 4% and 10% of the biomass in Chile and over 70% of the biomass in
315 the south African samples (Cerda and Castilla 2001, Fielding et al. 1994).
316 Clearly, intriguing differences among continents exist.
317
318 Studies that have contrasted the diversity and abundance of fauna associated
319 with invasive ecosystem engineers that replace native engineers have lacked
320 consistent outcomes, despite some taxa being very closely related. An
321 invasive hybrid cordgrass in the genus *Spartina* produced reductions in
322 mudflat infauna relative to the native *Spartina* it was replacing (Brusati and
323 Grosholz 2006). These authors attributed this reduction to pre-emption of
324 space owing to the extensive below-ground biomass associated with the
325 invader. McKinnon et al. (2009) uncovered an even more complex pattern for
326 native seagrasses (*Zostera capricorni* and *Halophila ovalis*) and the invasive
327 *Caulerpa taxifolia*. *Caulerpa* supported a lower abundance of infauna than the

328 seagrass, but the epifaunal response depended on the species of seagrass
329 and the location.
330
331 The context dependent nature of the impacts of invaders has been noted in
332 several studies and in some instance effects may be positive (e.g., Hacker
333 and Dethier 2006; Gribben et al. 2013). The scale over which impacts are
334 assessed can also modify interpretation. For example, it has been suggested
335 that a mosaic of invaded and non-invaded patches can increase regional
336 diversity (Byers 2002). At most invaded locations, *Pyura* currently creates a
337 mosaic of patches in which mussels and ascidians co-exist. We expect that
338 this pattern will likely increase diversity at the landscape scale. There were
339 exceptions, with some locations exhibiting monocultures of the invader (e.g.,
340 Twilight Beach Fig. 2A). We also note that *Pyura* can form extensive beds that
341 persist for time scales exceeding decades (e.g. in the case of *P. praeputialis*,
342 Castilla et al. 2004). These are the very conditions in which an ecosystem
343 engineer is likely to exert maximal influence (Jones et al. 2010).
344
345 The appearance of *Pyura* in New Zealand waters is concerning for several
346 reasons. First, this species is now well established in the north, having been
347 recorded from 22 locations (Jones et al. 2012 and authors unpublished data).
348 The presence of recruits indicates that this invader has developed self-
349 sustaining populations (authors' pers. obs.). Moreover, *Pyura* recruits were
350 not only present among ascidian clumps, they were also apparent in small
351 numbers among mussels; this may facilitate biotic replacement. Second,
352 there are indications that *Pyura* continues to move southwards with the two
353 most recent incursions on the east and west coasts (Okiato, Bay of Islands
354 and the entrance to Hokianga Harbour, respectively) being the most southern
355 recorded for this species. The invader is now firmly established in the four
356 major harbours of Northland – the Parengarenga, Houhora, Rangaunu and
357 Hokianga harbours. A recent review chronicling the invasion and spread of
358 invasive ascidians in the US notes that 97% of these invasive taxa have
359 continued to spread after their initial invasion (Simkanin et al. 2016), with the
360 hulls of vessels identified as an important vector of dispersal.
361

362 The third reason for concern, and very importantly, *Pyura* appears to be
363 tolerant of extremely wave-sheltered environments deep within natural
364 harbours. This stands in contrast with its congener *P. praeputialis* that is
365 restricted to wave-swept rock platforms in southern and southeastern
366 Australia (Knott et al. 2004; Rius and Teske 2013). Unfortunately, this
367 suggests that virtually every rocky shore in New Zealand has the potential to
368 support this invader, although whether it can form dense aggregations in calm
369 conditions remains unclear. The temperature regime in its native Australia is
370 consistent with its survival in most coastal regions of New Zealand's North
371 Island and the top of the South Island (Fletcher 2014).
372
373 The broader trophic implications of this ecosystem-wide shift are unknown.
374 Simberloff (2011) has noted that the impact of invaders may be subtle, but not
375 necessarily inconsequential. Potentially adding further complexity is the role
376 of native predators on the success of recent invaders. The large gastropod,
377 the cymatid *Cabestana spengleri* readily attacks and consumes *Pyura* in New
378 Zealand waters (Laxton 1971, authors' unpublished data). *Pyura praeputilais*
379 is also consumed in Australia and Chile by oystercatchers *Haemotopus* spp.
380 (Chafer 1994, authors' pers. obs.) and although oystercatchers were
381 observed foraging on New Zealand shores with *Pyura*, they were not
382 observed to consume them. The large native starfish, *Stichaster australis*, has
383 also been observed with stomachs overted over large specimens of *Pyura* at
384 the Bluff, a large rocky outcrop to the north of the study site (authors' pers.
385 obs.), although this predatory behaviour has not been recorded elsewhere.
386
387 Taken together, our findings are alarming. *Pyura* continues to spread
388 southwards, it appears to readily outcompete mussels for space on the
389 intertidal zone and is quite at home on sheltered as well as wave-exposed
390 rocky shores. The role of predators is curbing it's spread is currently unknown.
391 The continued spread of *Pyura* has implications for cultural and recreational
392 harvest of intertidal mussels as well as the wild-caught mussel-spat industry
393 which focuses on the Ninety Mile Beach area and supplies a large proportion
394 of New Zealand's mussel farming industry. At this stage it is hard to gauge
395 just how far reaching the shifts in assemblage structure and ecosystem

function associated with this invader will be. The extent to which change may ripple through other trophic levels in the ecosystem and a mechanistic understanding of the replacement of *Perna* by the invader remains a challenge for future work.

Acknowledgements

One of us (ARD) wishes to acknowledge support from the University of Auckland's Leigh Marine Laboratory visiting fellowship. We appreciate the assistance of the northern Iwi (Maori Land Council), particularly Laurie Austin and Louise Mischewski. Christine McComb, Errol Murray, Peter Browne, Brady Doak and Allison Broad ably assisted us in the laboratory or field. We wish to dedicate this contribution to the memory of Dr Bill Ballantine, a very strong advocate for the marine environment. This represents contribution number xxx from the ecology and genetics group, University of Wollongong. All collections and transportation of *Pyura* were made under the requirements imposed by the New Zealand Ministry for Primary Industries under Section 52 of the Biosecurity Act 1993.

Conflict of interest Declaration

The authors confirm that they have no conflicts of interest to declare.

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Table 1: Summary of 3-factor ANOVA for total diversity and abundance of motile fauna among clumps of a native mussel (*Perna canaliculus*) and an invasive ascidian (*Pyura doppelgangera*) on two rocky shore habitats at two locations. Factors were Location (random), Habitat (fixed) and Taxon (fixed), all with 2 levels, n=5. Significant effects (P<0.05) are highlighted in bold.

	Species Richness					Total Abundance			F versus
Source	DF	MS	F	P		MS	F	P	
Location	1	10.0	1.11	0.299		0.81	5.21	**0.03**	Residual
Habitat	1	8.1	0.14	0.772		1.46	18.97	0.14	Location x Habitat
Taxon	1	32.4	1.92	0.398		0.10	2.64	0.35	Location x Taxon
Location x Habitat	1	57.6	6.42	**0.016**		0.08	0.50	0.49	Residual
Location x Taxon	1	16.9	1.88	0.179		0.04	0.24	0.63	Residual
Habitat x Taxon	1	1.6	0.04	0.880		0.15	2.43	0.36	Location x Habitat x Taxon
Location x Habitat x Taxon	1	44.1	4.91	**0.034**		0.06	0.40	0.53	Residual
Residual	32	9.0				0.16			
Transform		none				LN (X+1)			
Cochran's C		0.241	ns			0.303	ns		

Table 2: Summary of 3-factor ANOVA for the percentage of the sample comprising molluscs and crabs or polychaetes among clumps of a native mussel (*Perna canaliculus*) and an invasive ascidian (*Pyura doppelgangera*) on two rocky shore habitats at two locations in northern New Zealand. Factors and replication are the same as those presented in Table 1. The Location x Taxon interaction was pooled. Significant effects (P<0.05) are in bold.

	Mollusc & Crab Abundance (% of sample)					Polychaete Abundance (% of sample)			F versus
Source	DF	MS	F	P		MS	F	P	
Location	1	737.1	6.33	**0.017**		38	0.4	0.53	1-Pooled Data
Habitat	1	32.5	0.03	0.883		83	0.4	0.64	Location x Habitat
Taxon	1	6741.3	57.90	**<0.0001**		11334	120.1	**<0.0001**	1-Pooled Data
Location x Habitat	1	947.1	8.14	**0.007**		210	2.2	0.15	1-Pooled Data
Location x Taxon	1	2.3	0.02	0.889		49	0.5	0.47	1-Pooled Data
Habitat x Taxon	1	71.9	2.70	0.348		34	0.2	0.76	Location x Habitat x Taxon
Location x Habitat x Taxon	1	26.6	0.23	0.636		224	2.4	0.13	1-Pooled Data
Residual	32	120.0				96			
1-Pooled Data	33	116.4				94			
Transform		Arcsin				Arcsin			
Cochran's C		0.413	*			0.368	ns		

Table 3: Summary of 3-factor ANOVA for the presence of *Corallina officinalis* (percentage of clump) for a native mussel (*Perna canaliculus*) and an invasive ascidian (*Pyura doppelgangera*) on two rocky shore habitats at two locations in northern New Zealand. Factors and replication are the same as those presented in Table 1. Significant effects (P<0.05) are in bold.

	Presence of *Corallina* (% of clump)				F versus
Source	DF	MS	F	P	
Location	1	0.09	0.11	0.739	Residual
Habitat	1	33.84	4.74	0.274	Lo x Ha
Taxon	1	77.01	9474.41	**<0.0001**	Residual
Location x Habitat	1	7.14	8.63	**0.006**	Residual
Location x Taxon	1	0.01	0.01	0.922	Residual
Habitat x Taxon	1	19.98	8.91	0.206	Location x Habitat x Taxon
Location x Habitat x Taxon	1	2.24	2.71	0.109	Residual
Residual	32	0.83			
Transform		Arcsin			
Cochran's C		0.299	ns		

Table 4: Summary of 3-factor PERMANOVA for the assemblage associated with clumps of a native mussel (*Perna canaliculus*) and an invasive ascidian (*Pyura doppelgangera*) on two rocky shore habitats at two locations in northern New Zealand. Factors and replication are the same as those presented in Table 1. Significant effects (P<0.05) are in bold, n=5.

Source	DF	MS	Pseudo-F	P (perm)	Unique Permutations
Location	1	4554.3	3.719	**0.001**	999
Habitat	1	4581.5	1.026	0.249	3
Taxon	1	38186.0	24.810	0.245	3
Location x Habitat	1	4466.6	3.647	**0.001**	999
Location x Taxon	1	1539.5	1.257	0.272	997
Habitat x Taxon	1	2868.1	0.803	0.521	18
Location x Habitat x Taxon	1	3569.1	2.914	**0.005**	998
Residual	32	1224.5			
Transform		none			

Table 5: Summary of SIMPER table from multivariate PERMANOVA analysis. Only taxa contributing 5% or more to the similarity of groups are included. Group M are the mussel, *Perna canaliculus* and Group P the ascidian *Pyura doppelgangera*.

Species	Group M Average abundance	Group P Average abundance	Average Dissimilarity	Diss / SD	Contribution %
Notoacmea sp.	18.05	0.5	17.4	1.83	21.13
Other errant polychaetes	1.15	12.2	11.1	1.54	13.54
Anthothoe	8.8	5.4	8.17	1.11	9.92
Perineries sp.	0.35	8.2	7.72	1.96	9.37
Risselopsis varia	0.5	6.0	4.77	0.53	5.79
Acanthochitonidae	2.05	6.3	4.47	1.58	5.42

Figure Captions

Figure 1. Study locations in Northern New Zealand, including the harbours mentioned in the text. Triangles indicated collection sites at Tauroa Peninsula and Shipwreck Bay.

Figure 2. *Pyura doppelgangera* in northern New Zealand, February 2014. A) An extensive band of the invasive ascidian in the mid to lower intertidal zone of Twilight Beach, B) clumps of the ascidian (lower left and left mid of quadrat) among the green-lipped mussel *Perna canaliculus* on emergent substrata at Tauroa Peninsula. Quadrat size 25 x 25cm.

Figure 3. A) Mean total Diversity (all taxa) and B) abundance of motile taxa among clumps of *Pyura doppelgangera* and *Perna canaliculus* in two habitat types at two locations in northern New Zealand. Locations; Tauroa Peninsula □ and Shipwreck Bay ■. Error bars are standard error of the mean, n=5.

Figure 4. Mean percentage of the total sample which were A) abundance of polychaetes and B) abundance of molluscs and crabs among clumps of *Pyura doppelgangera* and *Perna canaliculus* in two habitat types at two locations in northern New Zealand. Locations; Tauroa Peninsula □ and Shipwreck Bay ■. Error bars are standard error of the mean, n=5.

Figure 5. Mean abundance of sipunculids associated with clumps of *Pyura doppelgangera* and *Perna canaliculus* in two habitat types at two locations in northern New Zealand. Locations; Tauroa Peninsula □ and Shipwreck Bay ■. Error bars are standard error of the mean, n=5.

Figure 6. Abundance of flora and fauna associated with clumps of *Pyura doppelgangera* and *Perna canaliculus* in two habitat types at two locations in northern New Zealand. Locations; Tauroa Peninsula □ and Shipwreck Bay ■. The mean proportion of each clump supporting A) the coralline alga *Corallina officianalis* B) barnacles *Chaemosipho brunnea* and *C. columna,* C) Polychaetes forming calcareous tubes; serpulid (*Galeolaria hystrix),* sabellid (*Salmacina* sp.) and spirorbid tube worms. Error bars are standard error of the mean, n=5.

Figure 7. Ordination plot (nMDS) summarising community structure in clumps of *Pyura doppelgangera* (P) and *Perna canaliculus* (M) on emergent substrata (E) and shallow pools (P) in northern New Zealand. Locations have been pooled.

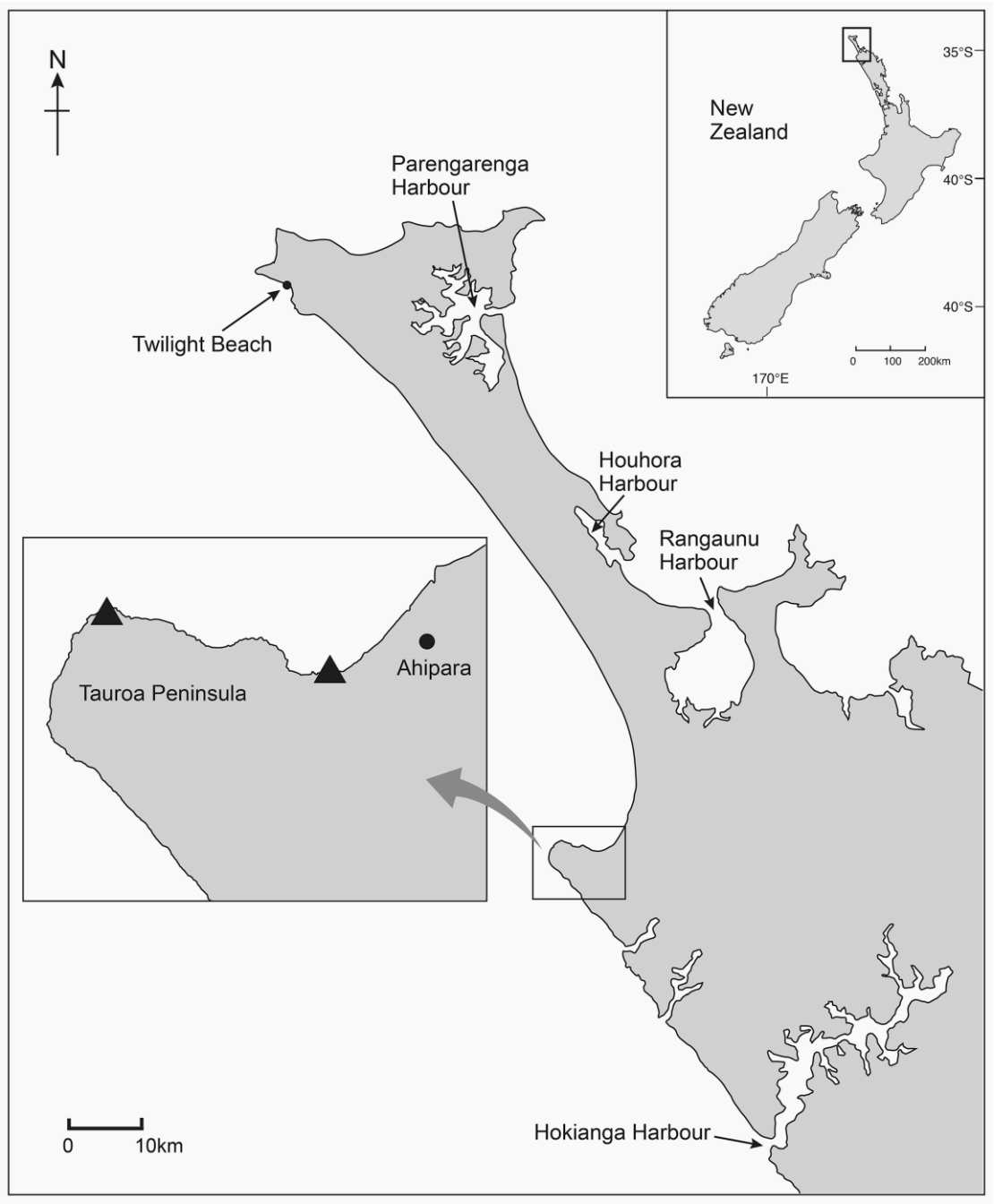
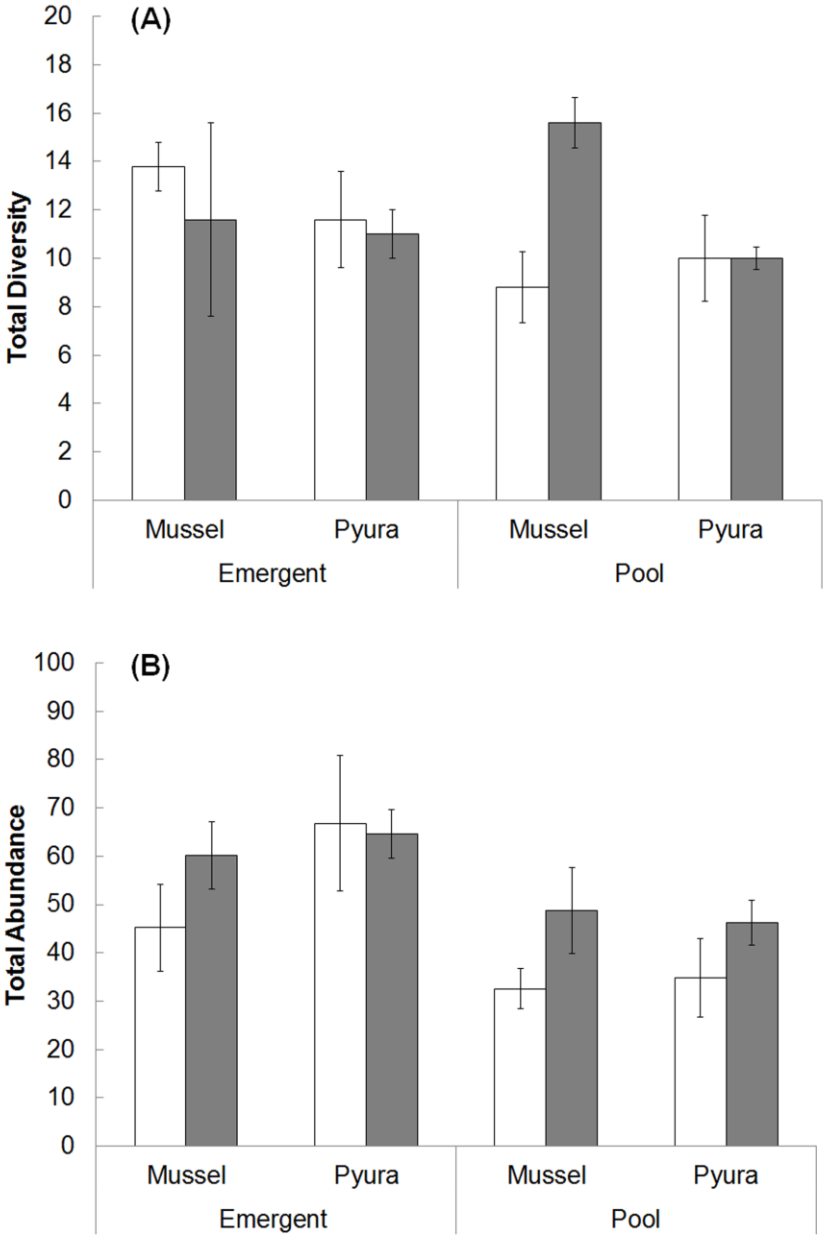

N
Parengarenga
Harbour
Twilight Beach
New
Zealand
35°S
40°S
40°S
0 100 200km
170°E
Houhora
Harbour
Rangaunu
Harbour
Tauroa Peninsula
Ahipara
0 10km
Hokianga Harbour

Fig. 1

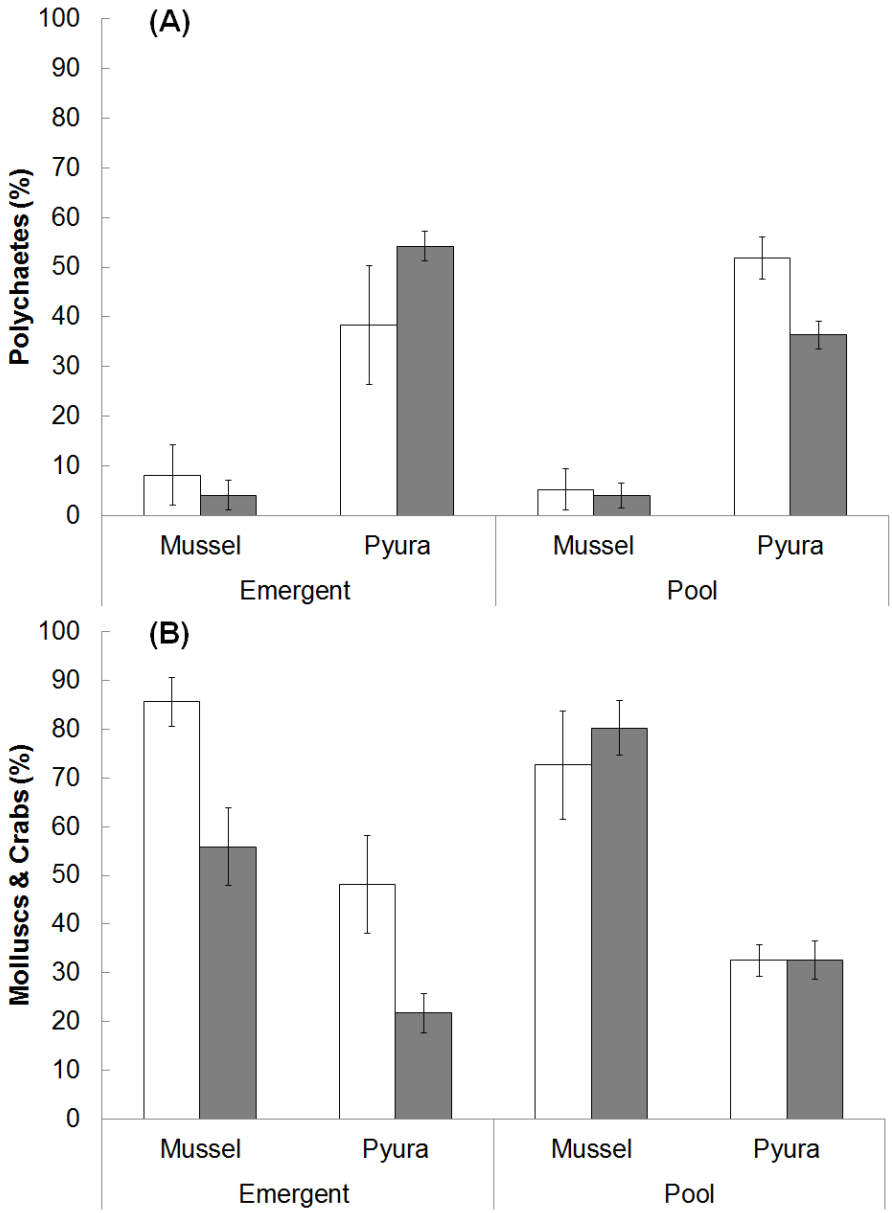
A)

B)

FIGURE 2


(A)
Total Diversity
20
18
16
14
12
10
8
6
4
2
0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool
(B)
Total Abundance
100
90
80
70
60
50
40
30
20
10
0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool

64
65 Fig. 3
66


(A)
Polychaetes (%)
100
90
80
70
60
50
40
30
20
10
0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool
(B)
Molluscs & Crabs (%)
100
90
80
70
60
50
40
30
20
10
0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool

67
68 Fig. 4
69

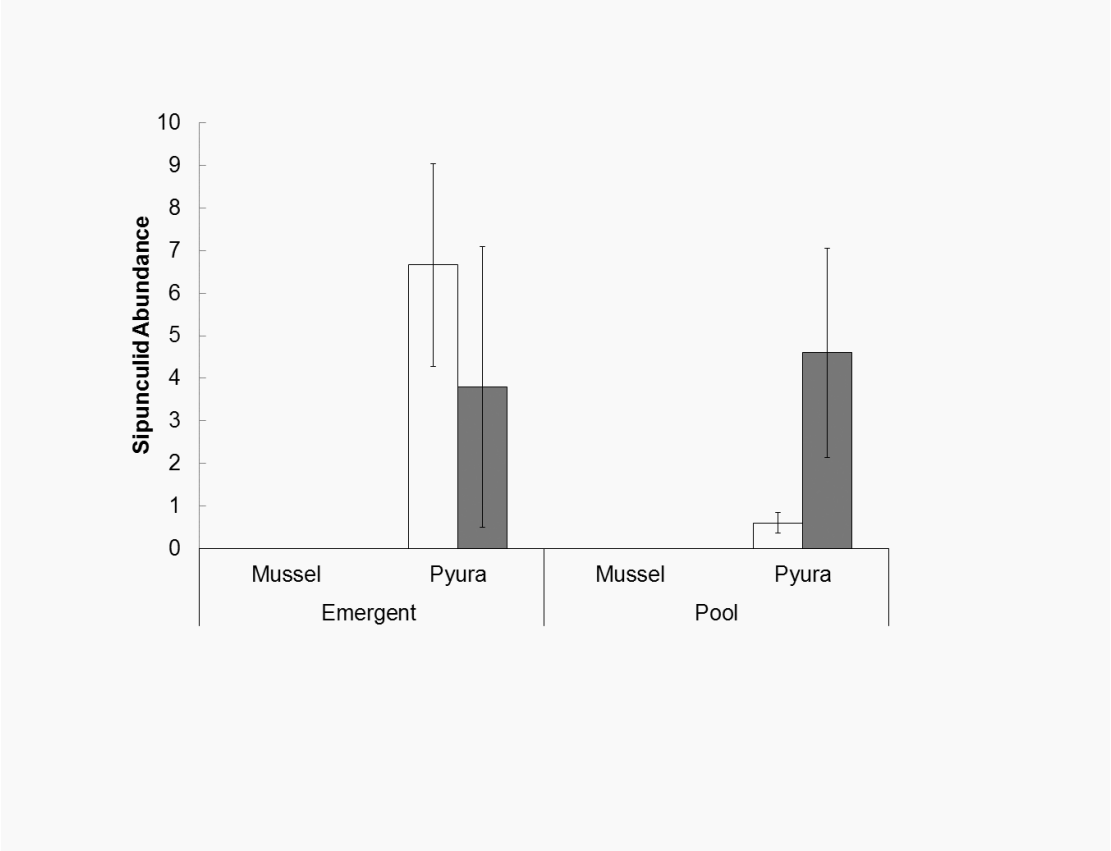
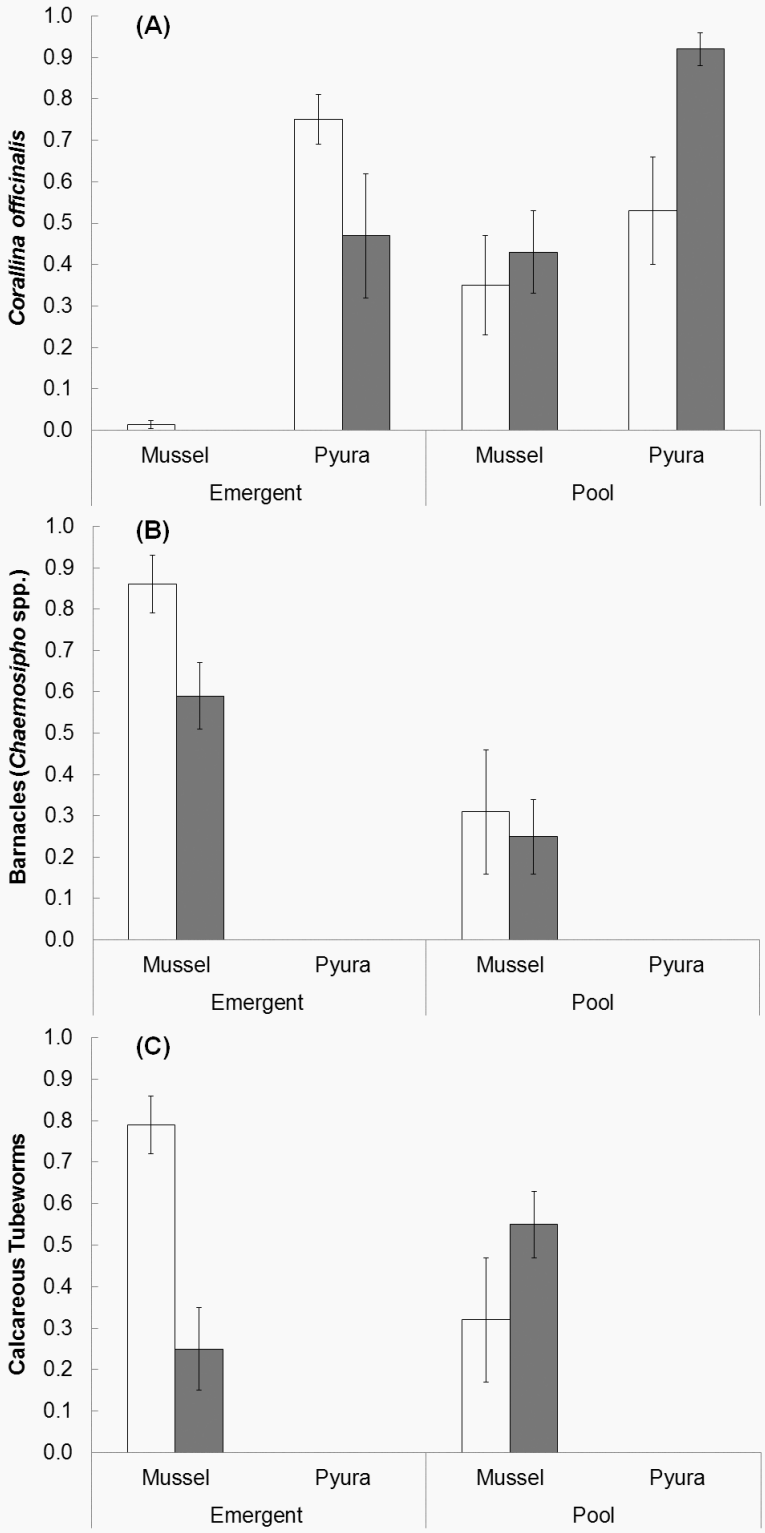
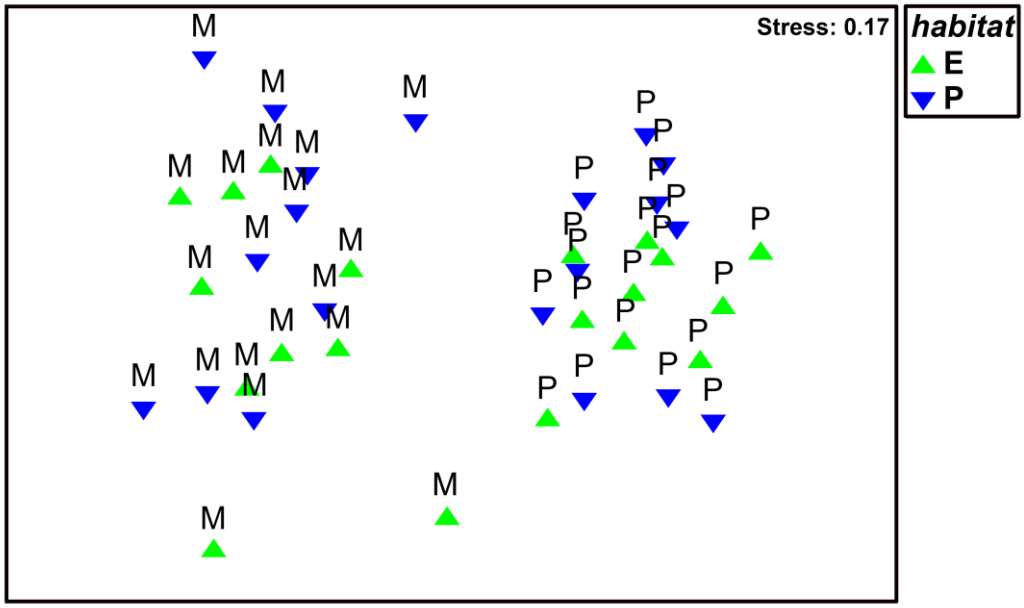

Sipunculid Abundance
10
9
8
7
6
5
4
3
2
1
0
Mussel
Pyura
Emergent
Mussel
Pyura
Pool

Fig. 5


(A)
Corallina officinalis
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool
(B)
Barnacles (Chaemosipho spp.)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool
(C)
Calcareous Tubeworms
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Mussel
Pyura
Mussel
Pyura
Emergent
Pool

74
75
76 Fig. 6



77
78
79 Fig. 7